Journal of Ethnobiology 24(2): 233–253 Fall/Winter 2004

SUBSISTENCE HUNTING BY THREE ETHNIC GROUPS OF THE LACANDON FOREST, MEXICO

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ABSTRACT.—This study compares hunting practices and preferences of Lacandon, Tzeltal, and Mestizo hunters from five communities adjacent to Montes Azules Biosphere Reserve in the Lacandon Forest, Chiapas, Mexico. We conducted interviews and directly observed animals taken by hunters during one year. Wildlife was hunted by most Indian and Mestizo residents primarily for food and to reduce crop damage. Per capita, Lacandon hunters extracted more wildlife biomass than both Tzeltal and Mestizo hunters. Total biomass extracted from 32 wildlife species was 8160 kg/year. Ungulates and rodents made up 87% of the total biomass harvested. Paca, red brocket deer, white-tailed deer, and collared peccary were the species with the greatest harvest rates. Harvest rates were positively correlated with the intrinsic rate of natural increase of species (r_{max}). Species that reproduce faster were hunted more frequently. There were no correlations between harvest rates and body mass, standing biomass, density, or local economic value of game species. Our results suggest that r_{max} of species should be considered when managing subsistence hunting and that hunting should be regulated, preferably through community-based management, for the benefit of both residents and local wildlife populations.

Key words: Chiapas, Lacandon Forest, Maya, Mexico, subsistence hunting.

RESUMEN.—El propósito de este estudio fue documentar y comparar las prácticas y preferencias de cacería de los residentes de la Selva Lacandona, Chiapas, México. Durante un año realizamos entrevistas y observamos las presas cobradas por cazadores lacandones, tzeltales y mestizos de cinco comunidades adyacentes a la Reserva de la Biósfera Montes Azules. La mayoría de los residentes indígenas y mestizos utilizaron la fauna para obtener alimento y reducir daños a sus cultivos. Los cazadores lacandones extrajeron más biomasa per capita de animales silvestres que los cazadores tzeltales y mestizos. La biomasa anual extraída de 32 especies fue de 8160 kg, 87% de la cual correspondió a ungulados y roedores. El tepezcuintle, el temazate, el venado cola blanca y el pecarí de collar fueron las especies con las mayores tasas de extracción. Las tasas de extracción se correlacionaron positivamente con la tasa intrínseca de incremento natural de la población (r_{max}). No se ha encontrado correlación entre las tasas de extracción y la masa corporal, biomasa en pié, densidad o valor económico local de las especies cazadas. Nuestros resultados sugieren que r_{max} debería considerarse a la hora de ma-

nejar la cacería de subsistencia y que la cacería debería ser regulada mediante el manejo comunitario y para beneficio de los usuarios y de las poblaciones locales de fauna silvestre.

RÉSUMÉ.—Cette étude documente et compare les pratiques et préférences de chasse des habitants de la forêt Lacandon au Chiapas, Mexique. Pendant une année, nous avons réalisé des entrevues et observé les animaux abattus par les chasseurs lacandons, tzeltals et métis de cinq communautés adjacentes à la Réserve de la Biosphère Montes Azules. La plupart des Métis et des Amérindiens chassent la faune principalement pour la viande et afin de réduire les dommages faits aux cultures. Les chasseurs lacandons prélèvent proportionnellement plus de biomasse que les chasseurs tzeltals et métis. La biomasse annuelle des 32 espèces chassées est de 8160 kg. Les ongulés et les rongeurs représentent environ 87 % de ce total. Les espèces les plus exploitées sont l'agouti, le daguet rouge, le cerf de Virginie et le pécari à collier. Le nombre d'animaux abattus est positivement corrélé au taux intrinsèque d'augmentation des espèces (r_{max}). Ainsi, les espèces dont le taux de reproduction est plus élévé sont chassées plus fréquemment. Toutefois, le nombre d'animaux abattus n'est pas corrélé à la masse corporelle, ni à la biomasse, ni à la densité, ni à la valeur économique allouée localement aux espèces. Les résultats de cette étude indiquent que le r_{max} des espèces devrait être pris en considération lors de la gestion de la chasse de subsistance. De plus, la chasse devrait être régulée par la communauté, au bénéfice des habitants et de la faune locale.

INTRODUCTION

Historically people have used wild animals for many purposes, such as food, clothing, medicine, tools, ritual objects, and companionship (Campbell 1983). Currently, hunting in rural areas is primarily for subsistence. We define subsistence hunting as the extraction of wild terrestrial vertebrates to obtain food, pelts, medicine, or other materials that are either consumed by the hunter and his family or exchanged for other goods (e.g., food, tools), but not sold in established markets (Ojasti and Dallmeier 2000; Redford and Robinson 1991; Stearman 2000).

In central and southern Mexico, rural communities have harvested wildlife for centuries. Ancient Aztec and Mayan Indians hunted many mammal, bird, and reptile species for meat, pelts, feathers, bones, fat, oil, pigments, medicine, and other materials that were either locally consumed or exchanged for other goods (Fagan 1984). Today, both indigenous and non-indigenous rural inhabitants of Mexican tropical forests regard wildlife as an important source of protein and hides (Escamilla et al. 2000; Jorgenson 1995; Mandujano and Rico-Gray 1991; Naranjo 2000). In the southeastern Mexican states of Campeche, Chiapas, Oaxaca, Quintana Roo, Tabasco, Veracruz, and Yucatán, the majority of people using wild animals are local farmers with low income, although there are a small number of sport hunters from the main cities. These local farmers are subsistence hunters who use wildlife primarily for meat, and they take the skin, heart, liver, stomach, brain, and other organs to feed themselves and their families. Occasionally, subsistence hunters sell the skins, fangs, and claws of large cats (i.e., jaguar, puma, and ocelot), the meat and hides of deer, peccaries, and pacas, and juvenile spider monkeys, parrots, scarlet macaws, and toucans to visitors from nearby cities or to local military troops (Guerra 2001). However, hunters do not involve them-

selves regularly in this commerce, because they know it is illegal and authorities may confiscate their guns (Naranjo 2002).

The preferences of subsistence hunters for different wildlife species are usually influenced by their main economic activity, access to domestic meat, ethnic origin, geographical isolation, local wildlife availability, and biological attributes of species (e.g., Hames and Vickers 1983). Subsistence hunters in neotropical rainforests often search for large-bodied species rather than for small animals, because of their greater quantities of meat and fat that yield more energy per unit effort (Bennett and Robinson 2000). However, hunters are more likely to encounter small, more abundant and productive species, and these animals usually make up their most common prey (Hill and Padwe 2000; Robinson and Bodmer 1999). Species such as peccaries, tapirs, deer, pacas, large primates, guans, curassows, crocodilians, iguanas, large turtles, and other large vertebrates are often the preferred species in neotropical rainforest, even though the most frequently hunted prey are often smaller species (Ayres et al. 1991; Bodmer 1995; Mena et al. 2000). In spite of their lower harvest rates, large-bodied animals usually make up the largest proportion of biomass extracted from terrestrial wildlife (Stearman 2000; Townsend 2000; Vickers 1991).

The Lacandon Forest of Chiapas is the southwestern sector of the Maya Forest and is one of the most important tracts of rainforest remaining in Mexico (Vásquez and Ramos 1992). It has large populations of vertebrates that are harvested by both indigenous and Mestizo subsistence hunters (Medellín 1994; Naranjo 2002). As in other parts of the neotropics, deforestation and overhunting in the Lacandon Forest are apparently impacting wildlife populations. However, these impacts need to be addressed further to find appropriate conservation strategies that consider both the human and wildlife components. This study compares the hunting practices by indigenous and Mestizo communities around Montes Azules Biosphere Reserve to determine the human component of subsistence hunting. Analyses test whether actual harvest rates are correlated with density, body mass, productivity, and economic value of wildlife species. This information is used to suggest appropriate conservation measures.

METHODS

Two localities adjacent to Montes Azules Biosphere Reserve (MABR) were studied (Figure 1). These study sites are located in the northeastern portion of the state of Chiapas (lat. 16°05′–17°15′N, long. 90°30′–91°30′W), which is delimited by the Guatemalan border on the east, north, and south, and by the Chiapas highlands on the west. The predominant climate of the Lacandon Forest is warm and humid with abundant summer rainfall (García and Lugo 1992). Average monthly temperatures range from 24°C to 26°C with maxima in May (28°C) and minima in January (18°C). Mean annual rainfall is 2500–3500 mm, with roughly 80% of the rain falling between June and November. The area was originally covered by over a million hectares of rainforest, of which about half remain. MABR is the largest protected area in the Lacandon Forest with over 3300 km^2. It harbors some of the largest Mexican populations of hardwood trees. Large-bodied vertebrate species still exist in the Lacandon Forest and are hunted by

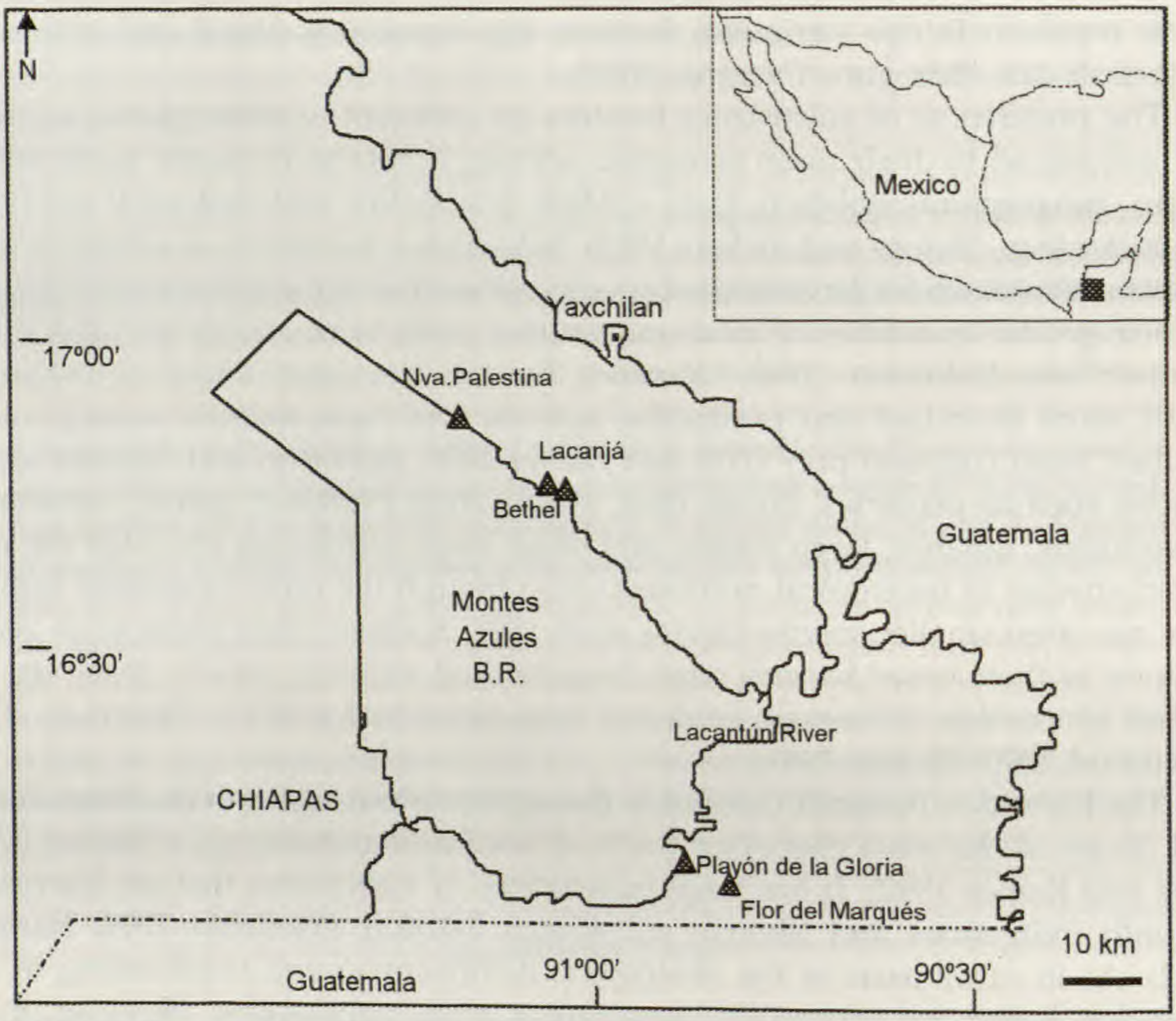

FIGURE 1.—Communities that participated in the study in the Lacandon Forest, Mexico.

both Indian and Mestizo residents (Medellín 1994; Naranjo 2002; Vasquez and Ramos 1992).

The first study site has three Indian communities of two different Mayan sociolinguistic groups: the Lacandon villages of Lacanjá-Chansayab (population 350) and Bethel (population 200) and the Tzeltal village of Nueva Palestina (population 15,000). Lacandon Indians have lived the study area for over three centuries (McGee 1990). They practice slash and burn agriculture (corn, beans, and squash), extraction of *Chamaedorea* palm leaves, fishing, hunting, and selling services and handicrafts to tourists (INI 1981; Naranjo 2002). Tzeltal Indians migrated from the highlands of Chiapas in the early 1970s and were relocated by the government in the community of Nueva Palestina. Their primary economic activities are both subsistence and commercial agriculture (corn, beans, and chili peppers) and cattle ranching. Subsistence hunting and fishing are complementary sources of food and income for the Tzeltal (Naranjo 2002).

The second study site includes the communities of Playón de la Gloria (population 300) and Flor del Marqués (population 200), which are inhabited by Mestizo immigrants from other regions of Chiapas and Oaxaca. These communities were founded in the mid-1970s and their residents farm corn, beans, chili peppers, cacao, and coffee. They also raise cows and pigs that they sell in the local market (Mariaca et al. 1997). Mestizo residents complement their diets by hunting and

TABLE 1.—Population size, number of hunters, and number of interviews conducted in five communities of the Lacandon Forest, Mexico (1999–2000).

	Bethel	Lacanjá-Chansayab	Nueva Palestina	Flor del Marqués	Playón de la Gloria
Ethnic Group	Lacandon	Lacandon	Tzeltal	Mestizo	Mestizo
Population	210	350	15,000	200	300
Hunters	30	50	850[b]	25	35
Interviews	44	43	45	44	56
Confidence interval (%)[a]	13.2	14.0	14.6	13.1	11.8
Catchment area (km^2)	113.1	201.1	452.4	28.3	28.3
Number of species used	35	37	32	42	37
Size rank	2	4	5	1	3
Isolation rank	3	5	4	1	2

[a] Calculations based on Krejcie and Morgan (1970); $\alpha = 0.05$ and $p = 0.50$.
[b] Only the 45 most active hunters were monitored during the study.

fishing (Naranjo 2002). The two Mestizo communities receive less economic and technical support from the government than the Lacandon and Tzeltal communities (Mariaca et al. 1997).

Hunting Patterns.—One of the authors (EJN) gathered information on wildlife use during multiple visits to the Lacandon Forest since the late 1980s. From September 1999 through August 2000 systematic records of hunting were collected through regular visits to the five communities. A total of 232 formal interviews were conducted (range: 40–56 per community) through structured questionnaires of men and women of age 15 or older. Although we interviewed between 12 and 22% of the total population in each village (except for Nueva Palestina), our confidence intervals (based on Krejcie and Morgan 1970) ranged from 11.8 to 14.6% in the communities visited (Table 1).

Field guides for birds (Howell and Webb 1995; Peterson and Chalif 1973) and mammals (Emmons and Feer 1997; Reid 1997) were used to help identify species during interviews. The active subsistence hunters were identified after the third visit to each community and they kept monthly records of their hunting. We asked people about the mammals, birds, and reptiles they hunted, as well as the hunting methods, sites, seasons, and uses of the animals. Only terrestrial vertebrates weighing 0.25 kg or more were used in this analysis. Two additional sources of information on hunting were the mammalian skulls and hides kept by hunters, as well visual records of people returning home with prey. Visual records include the species, sex, approximate age category (young, juvenile, or adult), weight, location and date of capture, and hunting method used. To improve the reliability of the results, only data from visual records of hunting are used in the numerical and statistical analyses.

Harvest Rates.—Catchment size is calculated as the area of a circle, centered on a village, with a radius of the maximum distance hunters were observed to travel. Harvest rate, determined from catchment area and hunting frequency, is the number of animals hunted/km^2/yr (Robinson and Redford 1991; Robinson and Bodmer 1999). Hunting effort, defined as the number of hunter-days/km^2/yr, is based

TABLE 2.—Hunting records and numbers of terrestrial vertebrate species used by residents from five communities of the Lacandon Forest, Mexico (1999–2000).

Classes	Number of species used		Visual hunting records	
	Data from interviews	Visual records	*n*	%
Mammals	29	19	626	80.1
Birds	15	9	148	18.9
Reptiles	6	4	8	1.0
Total	50	32	782	100.0

on data obtained through interviews and visual records. Relationships among the logarithmic values of harvest rates, body mass, metabolic biomass, r_{max}, economic value, and density are assessed with Pearson's correlation tests (Sokal and Rohlf 1995).

RESULTS

Hunting Patterns.—Fifty-one terrestrial vertebrate species were used by residents of the five communities visited during the study (Tables 2 and 3); we collected 782 visual hunting records (including 353 mammal skulls) of 32 species. Eighty percent of these records are of mammals ($n = 19$ species), 19% birds ($n = 8$), and 1% reptiles ($n = 5$).

To test whether Indian hunters take a wider diversity of species than Mestizo hunters, and whether residents of small and undeveloped villages rely more on wildlife than residents of larger, more developed communities, we compared the numbers of species between communities and ethnic groups. The number of species used by the five communities was tested against the size, isolation, and the percentage of residents interviewed in each community.

There were no differences in the numbers of species used between communities ($\chi^2 = 2.87$; $n = 5$; $p = 0.58$) and ethnic groups ($\chi^2 = 0.47$; $n = 3$; $p = 0.49$). The number of hunters is positively correlated with community population size (Pearson's $r = 0.99$; $n = 5$; $p < 0.0001$), but the numbers of species used is not correlated with community size, isolation, or percentage of residents interviewed ($p > 0.05$). The ten most frequently hunted species recorded in the interviews were: paca (*Agouti paca,* 92.5% of interviews), red brocket deer (*Mazama americana,* 89.6%), great curassow (*Crax rubra,* 87%), crested guan (*Penelope purpurascens,* 84.8%), collared peccary (*Tayassu tajacu,* 84.5%), nine-banded armadillo (*Dasypus novemcinctus,* 81.1%), great tinamou (*Tinamus major,* 79.9%), white-tailed deer (*Odocoileus virginianus,* 77.4%), coati (*Nasua narica,* 72.9%), and white-lipped peccary (*Tayassu pecari,* 61.5%).

Both Indian and Mestizo residents use wildlife primarily as a source of food (72.6% of interviewees), hides (3.2%), medicine (2.2%), raw materials for handicrafts (2.2%), and pets (1.4%). In addition, a considerable number people hunt animals to reduce damage to crops or to domestic animals (18.3%). Hunters from all five communities use primarily three hunting tools: 22-caliber rifles (38.8%),16-gauge shotguns (17.4%), and machetes (11.7%). Twenty-one percent of hunters

TABLE 3.—Terrestrial vertebrates used by residents from five communities of the Lacandon Forest, Mexico (1999–2000).

Taxa	English name	Part used	Purpose[a]	Record[b]
MAMMALS				
Didelphimorphia				
Didelphis marsupialis Linnaeus, 1758	Common opossum	meat	F, D	I, V
Philander opossum (Linnaeus, 1758)	Gray four-eyed opossum	meat	F, D	I, V
Xenarthra				
Tamandua mexicana (Saussure, 1860)	Northern tamandua	meat	F	I, V
Cabassous centralis (Miller, 1899)	Northern naked-tailed armadillo	meat, skin	F, C	I
Dasypus novemcinctus Linnaeus, 1758	Nine-banded armadillo	meat, skin	F, C	I, V
Primates				
Alouatta pigra Lawrence, 1933	Black howler monkey	meat, fat	F	I, V
Ateles geoffroyi Kuhl, 1820	Geoffroy's spider monkey	meat, fat	F, P, S	I, V
Carnivora				
Procyon lotor (Linnaeus, 1758)	Northern raccoon	meat	F, D, P	I, V
Nasua narica (Linnaeus, 1766)	White-nosed coati	meat	F, D, P	I, V
Potos flavus (Schreber, 1774)	Kinkajou	meat	F, P	I, V
Eira barbara (Linnaeus, 1758)	Tayra	meat	F, D	I
Conepatus semistriatus (Boddaert, 1784)	Hog-nosed skunk	meat, fat	F, M	I, V
Lontra longicaudis (Olfers, 1818)	neotropical river otter	meat, skin	F, C, S	I, V
Herpailurus yaguarondi (Lacépède, 1809)	Yaguarundi	skin	D, C, S	I
Leopardus pardalis (Linnaeus, 1758)	Ocelot	skin, fangs	D, C, S	I, V
Leopardus wiedii (Schinz, 1821)	Margay	skin	D, S	I, V
Panthera onca (Linnaeus, 1758)	Jaguar	skin, fangs, claws	D, C, S	I, V
Puma concolor (Linnaeus, 1771)	Puma	meat, skin, fangs, claws	F, D, C, S	I, V
Perissodactyla				
Tapirus bairdii (Gill, 1865)	Baird's tapir	meat, fat	F	I, V
Artiodactyla				
Tayassu pecari (Link, 1795)	White-lipped peccary	meat, skin, fat, fangs	F, C, S	I, V
Tayassu tajacu (Linnaeus, 1758)	Collared peccary	meat, skin, fat, fangs	F, D, C, S	I, V
Mazama americana (Erxleben, 1777)	Red brocket deer	meat, skin	F, C, S	I, V
Odocoileus virginianus (Zimmermann, 1780)	White-tailed deer	meat, skin, antlers	F, C, S	I, V

TABLE 3.—Continued.

Taxa	English name	Part used	Purpose[a]	Record[b]
Rodentia				
Orthogeomys hispidus (Le Conte, 1852)	Hispid pocket gopher	meat	F, D	I
Sciurus aureogaster Cuvier, 1829	Gray squirrel	meat	F	I, V
Coendou mexicanus (Kerr, 1792)	Mexican porcupine	meat, skin	F, C	I
Agouti paca (Linnaeus, 1766)	Paca	meat, fat	F, P, S	I, V
Dasyprocta punctata Gray, 1842	Central American agouti	meat	F, P	I, V
Lagomorpha				
Sylvilagus brasiliensis (Linnaeus, 1758)	Forest rabbit	meat, skin	F, C	V
BIRDS				
Tinamiformes				
Tinamus major (Gmelin, 1789)	Great tinamou	meat	F	I, V
Crypturellus boucardi (Sclater, 1860)	Boucard's tinamou	meat	F	I, V
Anseriformes				
Cairina moschata (Linnaeus, 1758)	Muscovy duck	meat	F	I
Falconiformes				
Micrastur semitorquatus (Vieillot, 1817)	Collared forest falcon	meat, feathers	F, C, S	I
Galliformes				
Ortalis vetula Wagler, 1830	Plain chachalaca	meat	F	I, V
Penelope purpurascens Wagler, 1830	Crested guan	meat, feathers	F, C	I, V
Crax rubra Linnaeus, 1758	Great Curassow	meat, feathers	F, C	I, V
Odontophorus guttatus (Gould, 1838)	Spotted wood-quail	meat	F	I
Columbiformes				
Columba spp. Linnaeus, 1758	Pigeon	meat	F	I, V
Psittaciformes				
Ara macao (Linnaeus, 1758)	Scarlet macaw	meat, feathers	F, P, C, S	I, V
Amazona autumnalis (Linnaeus, 1758)	Yellow-cheeked parrot	feathers	F, P, S	I, V
Amazona farinosa (Boddaert, 1783)	Blue-crowned parrot	feathers	F, P, S	I, V

TABLE 3.—Continued.

Taxa	English name	Part used	Purpose[a]	Record[b]
Strigiformes				
Pulsatrix perspicillata (Latham, 1790)	Spectacled owl	meat	F	I
Piciformes				
Pteroglossus torquatus (Gmelin, 1788)	Collared toucan	meat, bill	F, P, S	I
Ramphastos sulfuratus Lesson, 1830	Keel-billed toucan	meat, bill	F, P, S	I, V
REPTILES				
Testudines				
Dermatemys mawii Gray, 1847	White river turtle	meat, shell	F, C	I, V
Trachemys scripta (Schoepf, 1792)	Red-eared slider	meat, shell	F, C	I, V
Kinosternon spp.	Mud turtle	meat	F	I, V
Crocodylia				
Crocodylus moreletii (Dumeril & Dumeril, 1951)	Morelet's crocodile	meat, skin	F, C, S	I
Squamata				
Ctenosaura similis Gray, 1831	Spiny iguana	meat	F	I
Iguana iguana (Linnaeus, 1758)	Green iguana	meat	F, P, S	I, V
Boa constrictor (Linnaeus, 1758)	Boa	meat, skin	F, C, S	I, V

[a] C: craft for domestic use; D: avoid damage; F: food; M: medicine; P: pet; S: sale.
[b] I: interview, V: visual record.

TABLE 4.—Hunting effort estimated for three ethnic groups of the Lacandon Forest, Mexico (1999–2000).

	Lacandon	Tzeltal	Mestizo
Hunting events per month (A)[a]	5.1 (3.8)	1.2 (1.2)	4.2 (4.5)
Number of days per hunting event (B)[a]	2.0 (1.2)	3.5 (3.9)	1.3 (0.6)
Number of hunters (C)	80	850[c]	60
Capture area (km²) (D)	314.2	452.4	56.6
Effort (man-days/km²-year)[b]	31.1	94.7[c]	69.5

[a] Arithmetic means followed by standard deviations (in parenthesis).
[b] Effort: (A × 12 mo) (B × C)/D.
[c] If only the 50 most active hunters are considered, effort drops to 5.6 man-days/km²-year.

interviewed use trained dogs to stalk prey on a regular basis, and 13% of hunters prefer to stalk their prey at spots intentionally or naturally baited with native fruit (e.g., fruits of *Attalea butyracea, Licania platypus,* and *Pouteria sapota*). A few hunters (5.6%) construct rustic box-traps to capture pacas, guans, and tinamous.

Hunting activity is most intense during the dry season between November and March, when farmers have more spare time. The areas most commonly used for hunting are mature forests within communal lands near agricultural plots (58.5%), followed by cornfields and pasturelands (26.4%), secondary vegetation (14.1%), and mature forests inside MABR (1.0%). Estimates of hunting effort (man-days/km²-year) show that if all Tzeltal hunters of Nueva Palestina ($n = 850$) are considered, then effort expended by Indian and Mestizo hunters is similar. Mestizo hunters have a relatively high hunting effort, even though their catchment areas are much smaller than those of Indian communities. Lacandon hunters have lower effort than Tzeltal hunters if all hunters are considered. However, if only the most active hunters of Nueva Palestina ($n = 50$) are included, then Tzeltal hunters have a considerably lower hunting effort than both Lacandon and Mestizo hunters (Table 4).

Biomass Extracted and Harvest Rates.—The total biomass extracted from the 32 wildlife species hunted in all five communities was 8160 kg/year. Mammals account for 95.5% of the total biomass harvested, birds 3.9%, and reptiles 0.6% (Tables 5 and 6). Ungulates make up 66.6% of total biomass harvested, followed by rodents (20.8%), edentates (3.5%), cracids (3.4%), carnivores (2.6%), and primates (2.0%). The six species with the greatest total biomass harvested are paca (1674 kg; 20.5% of total biomass), red brocket deer (1469 kg; 18%), white-tailed deer (1137 kg; 13.9%), collared peccary (1130 kg; 13.8%), Baird's tapir (1050 kg; 12.9%), and white-lipped peccary (647 kg; 7.9%).

Mestizo hunters harvested fewer individuals ($\chi^2 = 254.1$; df = 36; $p < 0.0001$) and less biomass ($\chi^2 = 4126.9$; df = 36; $p < 0.0001$) than Lacandon and Tzeltal hunters. This is likely due to Mestizo hunters ($n = 60$) being greatly outnumbered by Indian hunters ($n = 930$) in this study. Total biomass harvested per hunter shows that Lacandon hunters took 41.1 kg/hunter, Tzeltal hunters took 4.0 kg/hunter and Mestizo hunters took 24.2 kg/hunter. Lacandon hunters extracted more biomass of red brocket deer, both peccary species, and paca. In contrast,

Tzeltal hunters took more biomass from paca, Baird's tapir, and white-tailed deer, while Mestizo hunters harvested more biomass from collared peccaries and pacas than from any other species (Tables 5 and 6).

Harvest rate of all species combined was 28.4 kg/ km^2/year. Collared peccary (23.2% of total biomass harvested per km^2), paca (17.7%), red brocket deer (16.5%), and white-tailed deer (12.2%) were harvested at greater rates than other species (Kruskal-Wallis' $H = 57$; df $= 31$; $p = 0.003$) (Table 7). Mestizo hunters harvested fewer individual animals per capita than Lacandon hunters, but they extracted game biomass at a rate 2.8 times greater than both Lacandon and Tzeltal hunters. This difference is due to the harvest rates of mammals; Mestizo hunters harvested collared peccaries, nine-banded armadillos, white-nosed coatis, jaguars, paca, red brocket deer, and white-tailed deer at greater rates than both Lacandon ($\chi^2 = 56.8$; df $= 18$; $p < 0.0001$) and Tzeltal ($\chi^2 = 64.2$; df $= 18$; $p < 0.0001$) hunters. The differences in harvest rates between Lacandon and Tzeltal hunters were slight, as were the harvest rates of birds and reptiles among the three ethnic groups ($p > 0.05$).

To investigate why some species are hunted more frequently than others we look at the correlates of hunting pressure, which include density, standing biomass, intrinsic rate of natural increase (r_{max}), body mass, and economic value. The correlations show that the most frequently harvested species (paca, nine-banded armadillo, and red brocket deer) were those with the highest values of r_{max}, that is, the most productive species ($r = 0.68$; df $= 12$; $p < 0.015$; Figure 2). However, there are no correlations between harvest rates and body mass, standing biomass, density, or economic value of wildlife species ($p > 0.05$).

DISCUSSION

Hunting Patterns.—Subsistence hunting is a predominantly opportunistic activity in the Lacandon Forest. Most residents of the study area are farmers and/or livestock raisers who take advantage of their visits to the croplands or pasturelands to hunt (Naranjo 2002). Three were few full-time hunters in the five communities visited, which may indicate that residents of the study area, under the current social and economic conditions, do not consider wildlife harvest very profitable. Hunting appears to be an important subsistence activity for the local people, since more than eight tons of wild meat were extracted by only five communities in a year. Most residents do not have enough money to buy meat every day, and not all raise domestic animals. Therefore, wildlife still represents a valuable resource in terms of protein for many people of the Lacandon Forest.

The number of wildlife species used did not differ significantly between communities. Previous studies have shown that indigenous groups tend to use more wildlife species than non-indigenous colonists (Redford and Robinson 1987). In this study, however, the Mestizo hunters of Flor del Marqués took more species than Tzeltal and Lacandon hunters. This is likely due to unequal government support for communication, education, health, and economic development among the rural communities of the Lacandon Forest. While some Lacandon (e.g., Lacanjá-Chansayab) and some Tzeltal communities (e.g., Nueva Palestina) have benefited from numerous subsidies, paved roads, electricity, and agroforestry proj-

TABLE 5.—Numbers of individuals and annual biomass harvested for 19 species of mammals extracted by three ethnic groups of the Lacandon Forest, Mexico (1999–2000).

Mammal taxon	Mean weight kg	Lacandon		Tzeltal		Mestizo		Total	
		n	kg	n	kg	n	kg	n	kg
Didelphis marsupialis	2	—	—	—	—	1	2	1	2
Tamandua mexicana	4	—	—	—	—	2	8	2	8
Dasypus novemcinctus	4	9	32	25	88	46	161	80	280
Alouatta pigra	5	15	75	—	—	1	5	16	80
Ateles geoffroyi	8	8	61	2	15	1	8	11	84
Procyon lotor	6	4	24	—	—	—	—	4	24
Nasua narica	5	7	32	—	—	5	23	12	54
Potos flavus	3	2	6	1	3	2	6	5	15
Eira barbara	5	1	5	—	—	—	—	1	5
Leopardus wiedii	4	3	11	4	14	1	4	8	28
Panthera onca	45	—	—	—	—	2	90	2	90
Tapirus bairdii	210	1	210	4	840	—	—	5	1050
Tayassu pecari	31	16	493	4	123	1	31	21	647
Tayassu tajacu	16	20	314	18	283	34	534	72	1130
Mazama americana	22	52	1123	8	173	8	173	68	1469
Odocoileus virginianus	42	4	168	19	800	4	168	27	1137
Orthogeomys hispidus	+	—	—	6	2	—	—	6	2
Agouti paca	6	75	450	172	1032	32	192	279	1674
Dasyprocta punctata	3	1	3	5	15	—	—	6	18
Total edentates		9	32	25	88	48	169	82	288
Total primates		23	136	2	15	2	13	27	164
Total carnivores		17	77	5	17	10	122	32	216
Total ungulates		93	2308	53	2219	47	906	193	5433
Total rodents		76	453	183	1049	32	192	291	1694
Total Mammals		218	3006	268	3388	140	1403	626	7797

+: < 0.5.

ects, many others (e.g., Flor del Marqués and Playón de la Gloria) have remained largely ignored (Mariaca et al. 1997). Indeed, the poorest hunters of the five communities relied more heavily on wildlife as a source of animal protein, hunted greater number of species, had higher mean harvest rates, and spent more time hunting. The relatively low effort expended by Lacandon hunters is likely due to their better economic situation, which allows them to hunt less than people in other communities; as a result they have a smaller impact on animal populations within their catchment areas.

Hunters consider ungulates, pacas, and cracids to be the most important game species. This agrees with hunting studies in other neotropical sites (Begazo 1999; Bodmer 1995; Jorgenson 1995; Robinson and Redford 1991; Vickers 1991). However, primates were not as important for hunters of the Lacandon Forest as they are in other places in Latin America (Mittermeier 1991; Redford and Robinson 1987). At least two factors may help to explain this difference. First, the Lacandon Forest is considerably poorer in primate species than South American forests. Second, Tzeltal and Mestizo hunters very rarely hunt monkeys because of cultural concerns ("monkeys look like small people"). In the past, Lacandon Indians hunt-

TABLE 6.—Numbers of individuals hunted and biomass harvested for 13 species of birds and reptiles used by three ethnic groups of the Lacandon Forest, Mexico (1999–2000).

Taxon	Mean weight kg	Lacandon		Tzeltal		Mestizo		All combined	
		n	kg	n	kg	n	kg	n	kg
Birds									
Tinamidae	1.1	5	5.5	—	—	1	1.1	6	6.6
Micrastur semitorquatus	0.8	1	0.8	—	—	—	—	1	0.8
Penelope purpurascens	2.5	29	72.5	5	12.5	—	—	34	85
Crax rubra	3.5	48	168	3	10.5	4	14	55	192.5
Ara macao	0.9	2	1.8	—	—	—	—	2	1.8
Amazona spp.	0.5	23	11.5	15	7.5	7	3.5	45	22.5
Strigidae	0.5	—	—	1	0.5	—	—	1	0.5
Ramphastos sulfuratus	0.4	4	1.6	—	—	—	—	4	1.6
Total Birds		112	261.7	24	31	12	18.6	148	311.3
Reptiles									
Dermatemys mawii	10	2	20	—	—	—	—	2	20
Trachemys scripta	1.5	—	—	—	—	2	3	2	3
Crocodylus moreletii	20	—	—	—	—	1	20	1	20
Ctenosaura similis	2.5	—	—	—	—	2	5	2	5
Iguana iguana	4	—	—	—	—	1	4	1	4
Total Reptiles		2	20	—	—	6	32	8	52
Total Vertebrates		332	3287.4	292	3418.6	158	1454.0	782	8160.0

ed and consumed primates (Baer and Merrifield 1971; March 1987), but our results suggest that these mammals are no longer important as food resources for the Lacandon. Likewise, Jorgenson (1995) found that young Mayan hunters of the Yucatán Peninsula hunted fewer monkeys than their parents and grandparents. Ayres et al. (1991) documented a decline in wild meat consumption due primarily to increased accessibility to the meat of domestic animals in a rural Brazilian community. It is likely that an analogous situation has occurred in the Indian communities of the Lacandon Forest, where dietary choices seemed to have shifted because of a higher availability of poultry, pigs, and canned meat.

Biomass Harvested and Harvest Rates.—About two-thirds of the total vertebrate biomass harvested comes from ungulates, which also are the most frequently hunted animals. Researchers in Quintana Roo (Jorgenson 1995) and Campeche (Escamilla et al. 2000), too, have found that ungulates are usually the most important vertebrate taken. In the Lacandon Forest, collared peccaries, white-tailed deer, and red brocket deer comprise most of the biomass harvested, while a lower biomass of tapir and white-lipped peccary is harvested due to their proportionally lower abundances in persistently hunted areas of southeastern Mexico. The white-tailed deer is taken at greater frequencies in the Yucatán Peninsula, where it is considerably more abundant than in the vicinities of MABR (Escamilla et al. 2000; Jorgenson 1995). Conversely, the paca is a more important food source for local hunters of the Lacandon Forest than for Mayan hunters of Campeche and Quintana Roo. By number of individuals (36% of total) and biomass extracted (21%), it represents the most important hunted animal in the Lacandon Forest. Although paca are persistently hunted and have a modest productivity (one or two young

TABLE 7.—Harvest rates (kg/10 km²-year) of 32 species of terrestrial vertebrates hunted by three ethnic groups of the Lacandon Forest, Mexico (1999–2000).

Species	Lacandon	Tzeltal	Mestizo	Total	%
Mammals					
Didelphis marsupialis	—	—	0.2	0.2	0.1
Tamandua mexicana	—	—	1.4	1.4	0.5
Dasypus novemcinctus	0.4	1.7	19.2	21.3	7.5
Alouatta pigra	1.0	—	0.4	1.4	0.5
Ateles geoffroyi	0.9	0.3	0.7	1.9	0.7
Procyon lotor	0.5	—	—	0.5	0.2
Nasua narica	0.4	—	4.0	4.4	1.6
Potos flavus	0.1	—	1.1	1.2	0.4
Eira barbara	0.1	—	—	0.1	+
Leopardus wiedii	0.2	0.3	0.6	1.1	0.4
Panthera onca	—	—	11.9	11.9	4.2
Tapirus bairdii	2.6	13.9	—	16.5	5.8
Tayassu pecari	6.2	2.7	2.7	11.6	4.1
Tayassu tajacu	4.5	5.9	55.5	65.9	23.2
Mazama americana	24.0	1.9	21.0	46.9	16.5
Odocoileus virginianus	2.9	13.0	18.6	34.5	12.2
Orthogeomys hispidus	—	+	—	+	+
Agouti paca	7.6	19.8	22.8	50.2	17.7
Dasyprocta punctata	—	0.3	—	0.3	0.1
Birds					
Tinamidae	0.1	—	0.2	0.3	0.1
Micrastur semitorquatus	+	—	—	+	+
Penelope purpurascens	1.6	0.3	—	1.9	0.7
Crax rubra	3.4	0.2	1.9	5.5	1.9
Ara macao	+	—	—	+	+
Amazona spp.	0.2	0.1	0.5	0.8	0.3
Strigidae	—	+	—	+	+
Ramphastos sulfuratus	+	—	—	+	+
Reptiles					
Dermatemys mawii	0.3	—	—	0.3	0.1
Trachemys scripta	—	—	0.5	0.5	0.2
Crocodylus moreletii	—	—	1.8	1.8	0.6
Ctenosaura similis	—	—	0.7	0.7	0.3
Iguana iguana	—	—	0.7	0.7	0.3
Total	57.1	60.5	166.4	283.9	100.0
Mean (std. dev.)	1.8 (4.5)	1.9 (4.7)	5.2 (11.5)	8.9 (16.9)	

+: < 0.05.

per year; Smythe 1983), they are widely distributed in the Lacandon study areas, and appear to tolerate hunting pressure and habitat disturbance (Emmons and Feer 1997). Hunters of all ethnic groups repeatedly mentioned that they like paca, due to the excellent taste of its fatty meat.

Redford and Robinson (1987) found that Indian hunters harvested wildlife at higher rates than colonists. However, Redford and Robinson's harvest rate is defined as the number of animals taken annually by a hunter. In this study, we define a community's harvest rate as the weight or number of animals taken

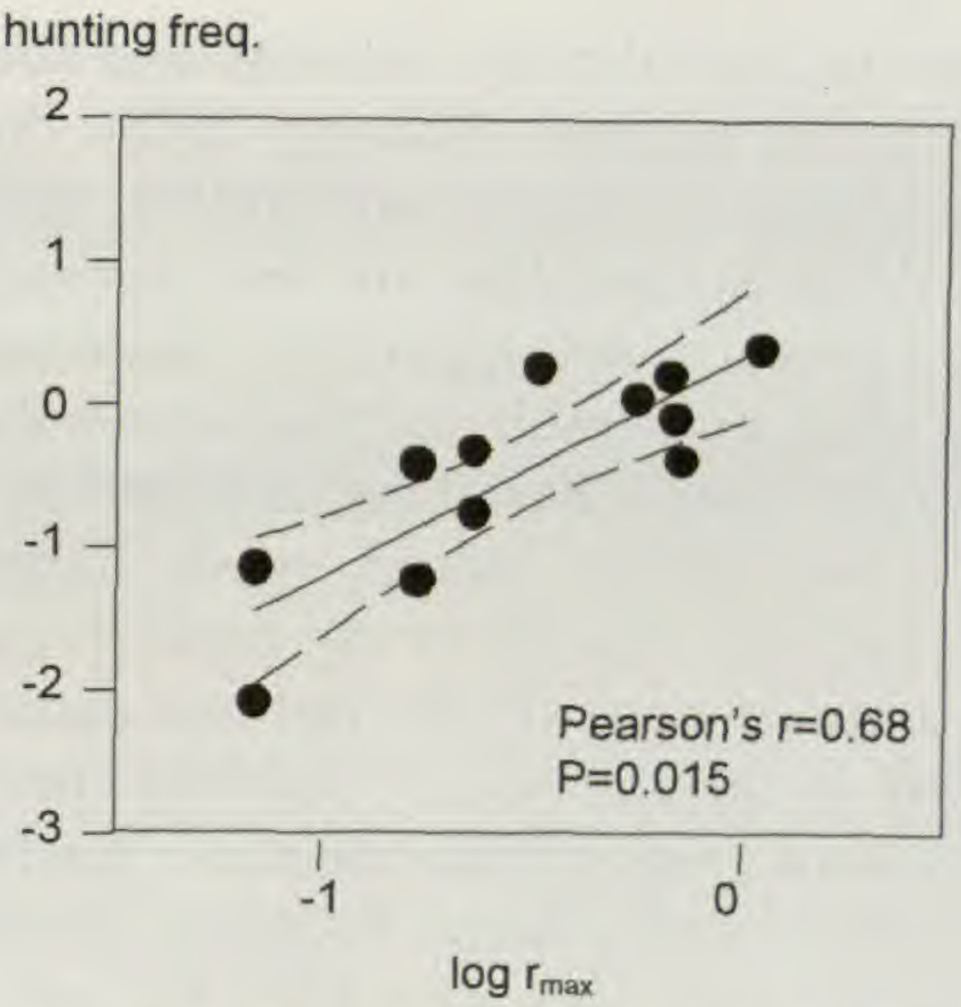

FIGURE 2.—Logarithmic correlation between intrinsic rates of natural increase (r_{max}) and harvest rates (individuals/year) of the 12 most important mammals hunted in the Lacandon Forest, Mexico.

annually in the catchment area (kg/km²/yr or number/km²/yr). Thus, using our own definition, we found that overall harvest rates of Mestizo hunters were higher than those of Indian hunters in the study area. Using Redford and Robinson's definition, our data suggest that Lacandon communities took more animals per consumer (or hunter) than Mestizo communities. The Tzeltal community is considerably larger and more populous than the other four villages, and it was not possible to keep records of all hunting events. Thus, only the most active hunters were surveyed (around 50 men) among the estimated 850 people who hunted in the community. It is very likely that wildlife biomass and harvest rates may have been underestimated in this village.

The average wildlife biomass harvested in the five communities was only 0.5 kg/person/year. However, if the largest community (Nueva Palestina) is excluded from this analysis, then the annual use of wildlife rises to 4.5 kg/person/year (5.9 kg/person/year for the Lacandon, and 2.9 kg/person/year for the Mestizo). These quantities are notably greater than the 1.8 kg/person/year estimated for the Mayan community of X-Hazil, Quintana Roo (Jorgenson 1995). The biomass consumed in the Lacandon Forest looks insignificant when compared to that consumed by the Sirionó Indians of eastern Bolivia (110 kg/person/year; Townsend 2000), the Huaorani of the Ecuadorian Amazon (61 kg/person/year; Mena et al. 2000), and the Aché of eastern Paraguay (45 kg/person/year; Hill and Padwe 2000). The relatively low consumption of terrestrial wildlife biomass by communities of the Lacandon Forest and the Yucatán Peninsula may be an indication that most rural people are involved in the market economy and obtain meat of domestic animals more easily and less expensively. The relatively low consumption also shows that there are a fewer full-time hunters; wildlife populations have been depleted, and now it is economically unprofitable to rely on wildlife as the main source of animal protein.

Impact on Wildlife Populations.—This study shows that hunting in the Lacandon Forest is determined not only by biological attributes of the species, such as their

reproductive productivity, but also by cultural and socioeconomic factors that influence the preferences of hunters (Naranjo 2002). Preferences of subsistence hunters appear to be having an impact on wildlife species in different ways in the Lacandon Forest. While species that are less vulnerable to overhunting (e.g., armadillo and collared peccary) are apparently maintaining healthy populations at persistently hunted sites, vulnerable species such as the tapir, the white-lipped peccary, and both primate species have been depleted by overexploitation or habitat fragmentation (Naranjo 2002). Indeed, many hunters interviewed for this study have noticed a constant decline of the most frequently harvested wildlife species around their communities over the last two decades. This decline in wildlife population has led to an increase in hunting effort and more man/hours hunting in larger catchment areas outside their own territories. This is particularly evident in the largest community, Nueva Palestina, where groups of 3–5 hunters occasionally spend up to seven days searching for prey more than 15 km from the community.

It is clear that subsistence hunting should be regulated for the benefit of both residents and wildlife populations of the Lacandon Forest. Under the current land tenure system in the area, a community-based management scheme (Bodmer and Puertas 2000) seems plausible for wildlife species, especially at Lacanjá-Chansayab, Bethel, and Nueva Palestina. These communities make up a large part of the intact rainforest of the Lacandon Forest. With the help of government agencies, conservation organizations, and local universities, people from key communities around MABR could be trained for planning and conducting model projects on sustainable wildlife use.

ACKNOWLEDGMENTS

We thank Allan Burns, John Eisenberg, Wayne King, Melvin Sunquist, George Tanner, Sophie Calmé, Brent Berlin, and Naomi F. Miller for their suggestions on the manuscript. Carlos Muench, Rausel Sarmiento, Isidro López, Romeo and Caralampio Jiménez, Antonio Navarro-Chankín and Celedonio Chan assisted in the fieldwork. Manuel Girón-Intzin reviewed Tzeltal names of species used. We are grateful to the residents of Playón de la Gloria, Flor del Marqués, Reforma Agraria, Nueva Palestina, Bethel, and Lacanjá-Chansayab for their hospitality during the fieldwork. Funds were provided by Mexico's National Council of Science and Technology (CONACYT), Mexico's National Commission for Biodiversity (CONABIO), the U.S. Fish and Wildlife Service, The Compton Foundation, the University of Florida's Program for Studies in Tropical Conservation (PSTC), the U.S. Man and Biosphere Program (MAB), and Idea Wild. El Colegio de la Frontera Sur (ECOSUR) facilitated with infrastructure, vehicles, and logistical support. The Dirección General de Vida Silvestre (INE-SEMARNAT) and the staff of Montes Azules Biosphere Reserve kindly gave the permits to carry out this project. Conservation International-Mexico, the Department of Wildlife Ecology and Conservation of the University of Florida, and the Universidad de Ciencias y Artes de Chiapas (UNICACH) provided material support in different ways.

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APPENDIX 1.—Local names of terrestrial vertebrates used by residents of the Lacandon Forest, Mexico. Tzeltal names are based on Aranda and March (1987), and Manuel Girón-Intzin (personal communication). Lacandon names are based on Aranda and March (1987), and Baer and Merrifield (1971). MN: Mestizo names are used for these species.

Taxon	Spanish name	Tzeltal name	Lacandon name	Mestizo name
MAMMALS				
Didelphimorphia				
Didelphis marsupialis	*tlacuache común*	***uch***	***ooch***	*tlacuache*
Philander opossum	*tlacuache cuatro ojos*	***uch***	***ooch***	*tlacuache cuatro ojos*
Xenarthra				
Tamandua mexicana	*hormiguero arborícola*	***tulan k'ab***	***chab***	*oso hormiguero*
Cabassous centralis	*armadillo cola desnuda*	***mail chan***	***wai-wech***	*armadillo*
Dasypus novemcinctus	*armadillo nueve bandas*	***mail chan***	***wech***	*armadillo*
Primates				
Alouatta pigra	*mono aullador negro*	***max saraguato***	***baa'ts***	*saraguato*
Ateles geoffroyi	*mono araña*	***max***	***mash***	*chango*
Carnivora				
Procyon lotor	*mapache*	***me'el***	***a'ka'bak***	*mapache*
Nasua narica	*coatí*	***wax***	***ts'oy***	*tejón, pizote*
Potos flavus	*martucha*	MN	***ak'a'mash***	*mico de noche*
Eira barbara	*tayra*	***me'el***	***sanjor***	*viejo de monte*
Conepatus semistriatus	*zorrillo espalda blanca*	***pai***	***pai***	*zorrillo*
Lontra longicaudis	*nutria*	***jaal-tz'i***	***tsura'ija***	*perro de agua*
Herpailurus yaguarondi	*leoncillo*	***choj***	***ek-barum***	*onza, gato de monte*
Leopardus pardalis	*ocelote*	MN	***ek-shush***	*tigre cangrejero*
Leopardus wiedii	*tigrillo*	***chin balam***	***chak'shikin***	*tigrillo*
Panthera onca	*jaguar*	***balam***	***barum***	*tigre*
Puma concolor	*puma*	***balam***	***chak-barum***	*león, puma*
Perissodactyla				
Tapirus bairdii	*tapir centroamericano*	***tzimin***	***c'ash-i-tzimin***	*danta, tapir*

APPENDIX 1.—Continued.

Taxon	Spanish name	Tzeltal name	Lacandon name	Mestizo name
Artiodactyla				
Tayassu pecari	*pecarí de labios blancos*	MN	***kekem***	*jabalí, senso*
Tayassu tajacu	*pecarí de collar*	***jalal***	***kitam***	*jabalí de collar*
Mazama americana	*venado temazate*	***chij***	***yuk***	*cabrito, temazate*
Odocoileus virginianus	*venado cola blanca*	***chij***	***ke***	*venado*
Rodentia				
Orthogeomys hispidus	*tuza*	***baj***	***baj***	*tuza*
Sciurus aureogaster	*ardilla gris*	***chuch***	***cu'uc***	*ardilla*
Coendou mexicanus	*puercoespín*	***wamal chitam***	***k'ish pach***	*puercoespín*
Agouti paca	*tepezcuintle*	MN	***jareu***	*tepezcuintle*
Dasyprocta punctata	*agutí*	MN	***tsub***	*cereque, guatuza*
Lagomorpha				
Sylvilagus brasiliensis	*conejo tropical*	***t'ul***	***tu'ur***	*conejo*
BIRDS				
Tinamiformes				
Tinamus major	*tinamú mayor*	***stzumut***	***ash***	*perdiz real*
Crypturellus boucardi	*tinamú*	***chin stzumut***	***nok'er***	*perdiz*
Anseriformes				
Cairina moschata	*pato real*	***pech'***	***cusa'***	*pato real*
Falconiformes				
Micrastur semitorquatus	*halcón de bosque*	***licawal***	***sic***	*gavilán*
Galliformes				
Ortalis vetula	*chachalaca*	***chachalaca***	***bach***	*chachalaca*
Penelope purpurascens	*cojolita, pava*	***x'uman***	***cosh***	*cojolita*
Crax rubra	*hocofaisán*	MN	***c'ambur***	*faisán*
Odontophorus guttatus	*codorniz*	***tzirim***	MN	*codorniz*
Columbiformes				
Columba spp.	*paloma*	MN	***ch'ic susuwir***	*paloma*

APPENDIX 1.—Continued.

Taxon	Spanish name	Tzeltal name	Lacandon name	Mestizo name
Psittaciformes				
Ara macao	*guacamaya roja*	MN	***yajaw t'ut***	*guacamaya*
Amazona autumnalis	*loro mejilla amarilla*	MN	***t'ut***	*perico*
Amazona farinosa	*loro cabeza azul*	MN	***jach t'ut***	*perico cabeza azul*
Strigiformes				
Pulsatrix perspicillata	*buho de anteojos*	***xoch***	***ikim***	*tecolote*
Piciformes				
Pteroglossus torquatus	*tucán collarejo*	MN	***pichik***	*tucán*
Ramphastos sulfuratus	*tucán cuello amarillo*	MN	***pin***	*tucán*
REPTILES				
Testudines				
Dermatemys mawii	*tortuga blanca*	MN	***jach ak***	*tortuga blanca*
Trachemys scripta	*tortuga jicotea*	MN	***s'in ak***	*jicotea*
Kinosternon spp.	*tortuga casquito*	MN	***majan ak***	*casquito*
Crocodylia				
Crocodylus moreletii	*cocodrilo de pantano*	MN	***ayim***	*cocodrilo, lagarto*
Squamata				
Ctenosaura similis	*iguana espinosa*	MN	***juj***	*garrobo*
Iguana iguana	*iguana verde*	MN	***juj***	*iguana*
Boa constrictor	*boa*	***chan***	MN	*mazacuata*